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Nonlinear responses of temperature sensitivities of community phenophases to warming and cooling events are mirroring plant functional diversity

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ABSTRACT

Lack of understanding of how plant diversity of different flowering functional groups mediates response patterns of community phenophases to climate change limits our ability to predict future phenology. We used reciprocal transplant experiments across four elevations (i.e., 3200, 3400, 3600 and 3800 m) on the Tibetan Plateau for three years to investigate how temperature change (i.e., warming and cooling) affects the temperature responses of plant functional diversity and community phenophases and their relationships. Our results showed that a nonlinear regression model was the best fitting model for most temperature responses of SDI and community phenophases under warming and cooling. Meanwhile, decreased diversity of early-spring flowering (ESF) and mid-summer flowering (MSF) groups under warming, and increased diversity of ESF under cooling, reduced temperature sensitivities of nearly all community phenophases. These results illustrate that changes in plant diversity should be taken into account when predicting the response pattern of temperature sensitivities of community phenophases.

1. Introduction

Phenology is an important ecological trait that is sensitive to climate change, especially to temperature (Menzel et al., 2011, 2006; Peñuelas et al., 2002; Rafferty and Ives, 2011; Wang et al., 2014a,b). Globally, most studies have found that climate warming significantly advanced the timing of most phenophases, and delayed senescence (Arft et al., 1999; Fu et al., 2015; Ladwig et al., 2016; Wang et al., 2014a,b; Wolkovich et al., 2012; Zhang et al., 2013). Although linear regression models have been identified as the major model that fits phenophase changes with temperature increase (Vitasse et al., 2009; Wolkovich et al., 2012), a growing body of studies have found responses of phenophases to continued warming or cooling spells that do not follow linear relationships (Iler et al., 2013; Jochner et al., 2016; Meng et al., 2016b; Morisette et al., 2009; Pope et al., 2013; Sparks et al., 2000). For example, long-term observations and warming experiments have found that temperature sensitivities of early phenophases decline with continued warming (Fu et al., 2015; Meng et al., 2016b). However, most reports of nonlinear phenological responses have been based on observations at the species level or observations of single phenological events (Iler et al., 2013; Jochner et al., 2016; Pope et al., 2013). Few studies have focused on responses of community phenophases, especially to cooling (Meng et al., 2016a, 2017).

Currently, nonlinear responses of plant phenophases to warming are attributed to plant adaptation to warming (Fu et al., 2015; Iler et al., 2013; Meng et al., 2016b; Piao et al., 2011; White et al., 1999; Wolkovich et al., 2014). Although temperature is an important factor influencing phenology, it does not entirely account for observed phenological changes, especially those of community phenophases (Forrest et al., 2010; Meng et al., 2017; Wolf et al., 2017). Biotic factors, such as plant evenness or richness, may also alter phenological responses of the plant community (Meng et al., 2017, 2016b; Wolf et al., 2017).Plant diversity (including evenness and richness) can be significantly altered by temperature changes (Tilman and Lehman, 2001; Alexander et al.,

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2015; Morisette et al., 2009; Suttle et al., 2007; Tylianakis et al., 2008; Wang et al., 2012). Thus, the interactive effects of temperature change and plant diversity change may have a much larger impact on plant community phenology than temperature change alone. We previously found that coverage changes of different flowering functional groups have a significant influence on community phenophases (Meng et al., 2017, 2016b). Especially, different species and functional groups can have divergent responses to temperature change, which may lead to a compensation effect that would affect community phenophases (Cleland et al., 2006, 2007; Wang et al., 2014b). Therefore, similar to species-level responses, we also hypothesized that the responses of community phenophases to climate change could be nonlinear, because species adapting to warming and cooling in different directions and magnitudes could cause a compensation effect on community phenophases.

To better understand the mechanisms involved in the effects of plant biodiversity change on temperature sensitivities of community phenophases under warming and cooling, we used reciprocal transplant experiments across four elevation gradients

(i.e., 3200, 3400, 3600 and 3800 m) and investigated: (1) whether the temperature responses of both plant community diversity and community phenophases have nonlinear responses to warming and/or cooling; and (2) the relationship between changes in plant diversity of different flowering functional groups and community phenophases under climatic change on the Tibetan plateau.

2. Materials and methods

2.1. Study sites and data collection

We used three continuous years of records of phenophases from alpine meadows at four elevation gradients (i.e., 3200, 3400, 3600 and 3800 m) at Haibei Alpine Meadow Ecosystem Research Station (HBAMERS), Qinghai province, China (37°37′ N, 101°12′ E) (Meng et al., 2017; Wang et al., 2014a,b). The alpine site is characterized by a short growing season, with green-up and senescence typically occurring in May and October, respectively. Twelve soil quadrats with 1 m × 1 m × 0.3–0.4 m depth (i.e., 0.3 m depth only at the 3800 m site due to the shallow soil layer) were dug each elevation (i.e., 48 quadrats for the four elevations in total) in early May 2007, and nine of them were randomly transferred to the other three elevations (i.e., three replicates at each elevation) (Meng et al., 2017; Wang et al., 2014a). To insulate from the effects of nutrient exchange and root invasion from the surrounding environment, all the soil quadrats were sealed by impervious materials.

The observational quadrat (1 m × 1 m) was segmented into 100 grid cells. Species richness and evenness were monitored at each point in mid-August of every year using the quadrat method. All species were divided into three categories based on their flowering time (i.e., early-spring (ESF, blooming before June), mid-summer (MSF, blooming between June and July) and late-autumn flowering (LAF, blooming after July) functional groups as detailed in Meng et al. (2016a, 2017). The frequency of sampling from 2008 to 2010 to examine community phenological sequences was 3–4 days, monitoring each species phenology occurring on the 100 points. The phenological sequences were divided into 7 phenophases, including onset of leaf-out (OLO, emergence of visible leaf), first flower bud (FB, emergence of unopened blossom bud), first flowering (FF, emergence of bloom), first fruiting-set (FFS, emergence of fruit), post-fruiting vegetation (OPFV, date of end fruiting), first leaf-coloring (FLC, emergence of leaf coloring) and complete leaf-coloring (CLC, complete leaf coloring). The timing of each phenophase was the date on which 15% of the observed species experienced the phenological event. CLC was the date on which 95% of observed species had completed senescence (Meng et al., 2017, 2016b).

Soil temperature and soil moisture were continuously monitored from 2008 to 2010 (soil temperature in Fig S1, Wang et al., 2014b). Mean annual soil temperatures at 5 cm depth were 3.9, 2.5, 2.0, 0.4 °C and mean annual soil moistures at 20 cm depth were 26%, 21%, 30% and 8% across the four increasing elevations, respectively (Wang et al., 2014a,b). Temperature change is the difference between original site and transferred site for transplanted plants at each year.

2.2. Computation of temperature sensitivities of Simpson's Diversity Index (SDI), community phenophases and accumulated soil temperature (AST)

Different species and functional groups have divergent response magnitudes and directions, their mutual compensation effect could shape community phenophases. Therefore, changes in species richness and evenness (i.e., plant diversity) of functional groups could reshape community phenophases due to their divergent phylogeny. SDI was used to quantify the plant diversity of the community, which consists of species richness and evenness (1). The AST of community phenophases was the sum soil temperature remaining above 0 °C (2). Downward and upward transfer represented warming and cooling, respectively. Positive and negative values represent an increase and decrease in SDI per 1 °C change or delay and advance of phenophases in days per 1 °C change under the transferred treatments, respectively.

$$SDI = 1 - \sum_{i=1}^{s} \left(\frac{n}{N}\right)^2 \quad (1)$$

$$AST = \sum_{t=0}^{ph} (T_t - 0) \; if \; T_t > 0 \quad (2)$$

$$TS = \frac{DCP}{Td} \quad (3)$$

where s is species richness in a certain flowering functional group, n is the total individual number of a particular species in a certain flowering functional group, and N is the total individual number of a certain flowering functional group. The value of SDI ranged between 0 and 1. t = 0 is the first date on which the 5 cm depth soil temperature remained above 0 °C for five continuous days; ph is the date of a particular community phenophase; T_t was 5 depth soil temperature remained above 0 °C during the date of t = 0 and ph; TS is the temperature sensitivity of SDI, AST and community phenophases; DCP is the differences of SDI, AST and community phenophases, and Td is the temperature difference.

2.3. Data analysis

We used a general linear model to test the effects of treatments and their interactions on the temperature responses of SDI of different flowering functional groups and of community phenophases in SPSS version 23. We adopted Type III SS.

We used linear and nonlinear regressions to fit the responses of temperature sensitivity of SDI, of community phenophases and of AST to temperature changes. The linear model was fitted by the function lm (). The nonlinear model was analysed by the package Segmented in R. We used Akaike's Information Criterion (AIC) to compare the fitness of two different models (Migliavacca et al., 2012; Richardson et al., 2013; Turkheimer et al., 2003). The smaller the AIC, the better the fit. Meanwhile, the P value (< 0.05) was used to examine the significance of each linear regression. These functions and packages were performed in R 3.3.3 (R.C. Team, 2017). We calculated partial correlations between temperature responses of SDI and temperature sensitivities of community phenophases, setting temperature changes as the controlling variable, to explore the effects of SDI on community phenophases. Because the community phenophases were calculated based on all monitored species in 100 points. Therefore, changes in plant diversity (including species richness and evenness) could affect community phenophases. There was incomplete data at 3600 m due to partial destruction of the experimental site in 2009 and complete destruction in

Table 1
General linear model used to test the effects of treatment and their interactions on temperature responses of SDI for different flowering functional group over three years.

Source of variation	SDIESF			SDIMSF			SDILAF		
	d.f.	*SS*	*P*	d.f.	*SS*	*P*	d.f.	*SS*	*P*
Year (Y)	2	0.005	0.406	2	0.016	**0.040**	2	0.013	0.744
Donor site (D)	3	0.109	**0.000**	3	0.042	**0.001**	3	0.022	0.796
Receptor site (R)	3	0.100	**0.000**	3	0.091	**0.000**	3	0.025	0.765
Y*D	5	0.009	0.679	5	0.025	0.072	5	0.016	0.979
Y*R	4	0.028	0.051	4	0.017	0.137	4	0.062	0.575
D*R	5	0.148	**0.000**	5	0.020	0.137	5	0.005	0.999
Y*D*R	4	0.028	0.050	4	0.015	0.185	4	0.007	0.987
Error	54	0.149		54	0.124		54	1.155	

Note: SDIESF, SDIMSF and SDILAF represent the temperature responses of Simpson's Diversity Index of early-spring, middle-summer and late-autumn flowering groups, respectively.
The numbers in bold are significant at the level of 0.05.

2010 by plateau pika (*Ochotona curzoniae*).

3. Results

3.1. Nonlinear temperature sensitivities of Simpson's Diversity Index (SDI) under temperature change

Temperature sensitivities of Simpson's Diversity Index for early-spring (SDIESF) and mid-summer flowering species (SDIMSF) were mainly affected by donor site and receptor site ($P < 0.05$, Table 1). However, the temperature sensitivity of SDI for late-autumn flowering species (SDILAF) was not significantly affected by these treatments (Table 1). We found that warming significantly decreased the SDI for ESF and increased SDIs for ESF and MSF (Table S2, Fig. 1). However, other functional groups were non-significantly changed under warming and cooling (Table S2, Fig. 1). Furthermore, we found that nonlinear regression models were the best fitting models for SDIESF and SDIMSF under warming and/or cooling, while no significant regression model was identified for SDILAF (Table S1). Generally, SDIESF and SDIMSF were significantly increased under cooling and decreased under warming and/or cooling, respectively (Figs. 1 and S2. Moreover, SDIESF and SDIMSF were significantly decreased under warming and/or cooling before the breakpoints (Tables S1and S2, Fig. 2). Beyond the breakpoints, they remained relatively stable (Tables S1 and S2, Fig. 2).

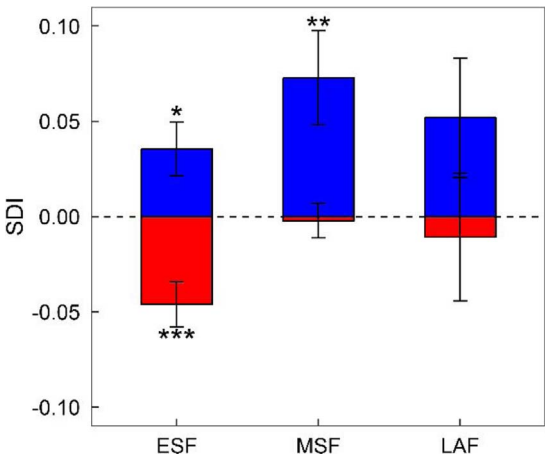

Fig. 1. Changes in Simpson's Diversity Index for three different flowering functional groups under warming and cooling. Blue and red columns represent cooling and warming, respectively. ESF, MSF and LAF represent early-spring, mid-summer and late-autumn flowering groups, respectively. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

These breakpoints were 0.85 °C for temperature sensitivity of SDIESF and 0.63 °C for SDIMSF under warming, and −1.31 °C for SDIESF under cooling (Tables S1 and S2, Fig. 2).

3.2. Nonlinear temperature sensitivities of community phenophases

Temperature sensitivities of community phenophases were significantly affected by year, donor site, receptor site, different phenophases and their interactions ($P < 0.001$, Table 2). We found that nonlinear regressions were the best fitting models based on ΔAIC of two models, except for first fruit-set for forbs or seeding-set for graminoids (FFS) under cooling and first leaf coloring (FLC) under warming (Tables S1 and S2, Fig. 3). In general, their mean breakpoints were around ± 0.65 °C under warming and cooling (Tables S1 and S2, Fig. 3). The temperature sensitivities of all AST associated with community phenophases had nonlinear responses to temperature changes (Fig. 4). Their mean breakpoints were 0.91 °C under warming and −0.75 °C under cooling (Tables S3 and S4, Fig. 4).

3.3. Relationships between temperature responses of SDI for different flowering functional groups and onsets of community phenophases

We found changes in SDI of different functional flowering groups, rather than changes in SDI of community, were a predictor of changes of community phenophases (Tables 3 and S5). Temperature responses of SDIESF and SDIMSF had significantly positive correlations with nearly all temperature sensitivities of onsets of the community phenophases, except for CLC which had significant negative correlations under warming (Table 3). For cooling, the temperature responses of SDIESF had significantly positive correlations with the temperature sensitivities of three early phenophases (onset of leaf-out (OLO), first flower bud (FB) and first flowering (FF)), and negative correlations with the temperature sensitivities of onsets of the four other phenophases (i.e., FFS, OPFV, FLC and CLC) (Table 3). There were significant negative correlations between the temperature responses of SDIMSF and FB, FFS, OPFV and FLC, whereas the temperature responses of SDILAF had significantly positive correlations with the temperature sensitivities of the onsets of FFS and OPFV (Table 3).

4. Discussion

Our study revealed that most temperature sensitivities of Simpson's Diversity Index (SDI) and temperature sensitivities of the onsets of community phenophases had nonlinear responses to warming and cooling. Furthermore, most temperature sensitivities of Simpson's Diversity Index for the early-spring flowering functional group (SDIESF) and mid-summer flowering functional group (SDIMSF) had significantly positive or negative correlations with the temperature sensitivities of the onsets of community phenophases. Therefore, our results suggest that ecological and evolutionary constraints could affect the responses of the temperature sensitivity of the onsets of community phenophases to temperature changes (Cleland et al., 2006; Hollister et al., 2005; Sherry et al., 2007; Steltzer and Post, 2009).

4.1. Temperature responses of SDI for different flowering functional groups affect the temperature sensitivities of community phenophases

Some field experimental studies have found that changes in species losses and coverage have significant influence on phenophases (Meng et al., 2017, 2016b; Wolf et al., 2017). Although alpine plants are adapted to low temperature, they still survive under their thermic optimum (Tieszen et al., 1981). Although warming should facilitate individual plant development in cold-limited ecosystems, that same warming may also increase interspecies competition which could lead to decreased plant diversity at the community level. We found that decreased temperature responses of SDIESF and SDIMSF could

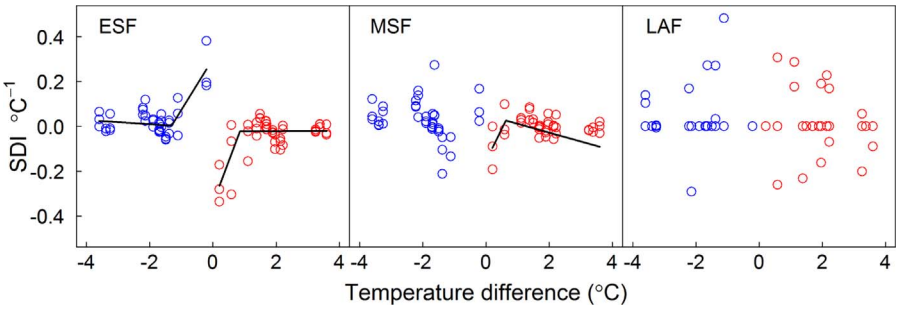

Fig. 2. Nonlinear regressions between the temperature sensitivities of Simpson's Diversity Index (SDI) and soil temperature differences. Each point represents temperature sensitivities of SDI from one plot at specific year (6 and 33 for warming or 30 for cooling on two sides). Blue and red points represent cooling and warming, respectively. The temperature change is difference between original site and transferred site for transplanted plants. ESF, MSF and LAF represent early-spring, mid-summer and late-autumn flowering groups, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 2
General linear model used to test the effects of treatments and their interactions on temperature sensitivities of community phenophases over three years.

Source	SS	d.f.	Sig.
Year (Y)	1521.768	2	0.000
Donor site (D)	12,272.221	3	0.000
Receptor site (R)	8090.389	3	0.000
Phenophases (P)	2564.438	6	0.000
Y * D	1948.298	5	0.000
Y * R	1941.564	5	0.000
Y * P	1687.043	12	0.000
D * R	10108.079	5	0.000
D * P	15086.676	18	0.000
R * P	9692.502	18	0.000
Y * D * R	2207.280	6	0.000
Y * D * P	5242.837	30	0.000
Y * R * P	4407.585	30	0.000
D * R * P	15787.624	30	0.000
Y * D * R * P	7242.266	36	0.000
Error	1474.018	420	

significantly advance the timings of 6 community phenophases and delay CLC because of positive and negative correlations between them under warming (Table 3). This might be attributed to decreased SDI reducing competition among species in the same flowering functional group, because the same flowering functional group had similar phenological traits (Meng et al., 2016a, 2017, 2016b; Wang et al., 2014a,b). Plant development was generally restricted by limited resources in alpine area, such as temperature, nutrients, energy and niche (Arft et al., 1999; Wolkovich and Cleland, 2014; Jiang et al., 2016; Wolf et al., 2017). Decreased SDI due to competition therefore could contribute to ensuring the remaining species acquire relative adequate resources under warming.

The stress gradient hypothesis has shown that interspecies competition could turn to facilitation along with increasing cold stress (Bertness and Callaway, 1994; Leverett, 2017). Furthermore, facilitation contributes to protecting plant diversity (Cavieres and Badano, 2009; Valiente-Banuet et al., 2006). Consistent with these studies, our results support this hypothesis, because we found that cooling significantly increased the plant diversity of ESF and MSF (i.e., SDI, Fig. 1). However, the increased temperature sensitivity of SDIESF significantly delayed three early community phenophases (i.e., OLO, FB and FF) because of positive correlations between them under cooling. This may be because ESF had a higher sensitivity to cooling than MSF (Wang et al., 2014a). Hence, increased SDIESF could delay these early community phenophases under cooling. However, increased SDIESF and SDIMSF could significantly advance the four other community phenophases (i.e., FFS, OPFV, FLC and CLC) because of negative correlations between them under cooling (Table 3). SDILAF had little effect on the two community phenophases (i.e., FFS and OPFV), despite significant positive correlations, due to its low percentage in the community (< 1%) (Meng et al., 2016a, 2017). These results may partly explain the lower temperature sensitivities of late community phenophases compared with early community phenophases under cooling

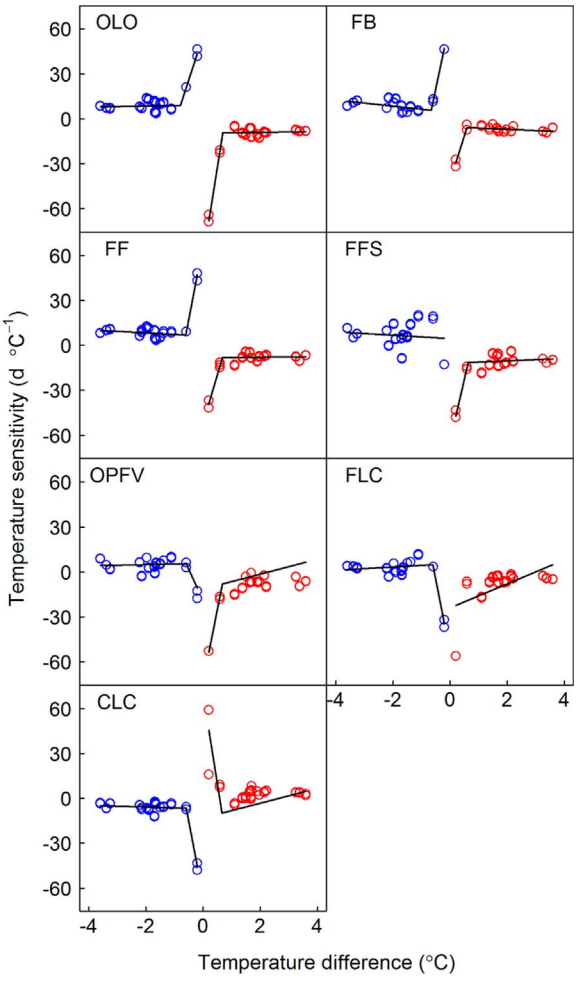

Fig. 3. Nonlinear and linear regressions between temperature sensitivities of community phenophases and soil temperature differences. Each point represents temperature sensitivities of community phenophases from one plot at specific year (6 and 33 for warming or 30 for cooling on two sides). Blue and red lines represent cooling and warming, respectively. The temperature change is difference between original site and transferred site for transplanted plants. OLO, onset of leaf-out; FB, first flower bud; FF, first flowering; FFS, first fruit-set for forbs or seeding-set for graminoids; OPFV, onset of post-fruiting vegetation; FLC, first leaf coloring and CLC, the date of complete leaf-coloring. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(Meng et al., 2017). In this way, FFS could have enough time to ensure seed maturation, because the life strategy of plants in high cold regions tend to invest most resources in the reproductive stage to occupy more bare land or temporal niches (Arft et al., 1999). The slightly delay in onset of late community phenophases (i.e., OPFV and FLC) and a significant delay in CLC prolonged the coloring stage, which may contribute to nutrient resorption, because nutrient resorption often occurs when chlorophyll declined (Hoch et al., 2001; Norby et al., 2000). Thus,

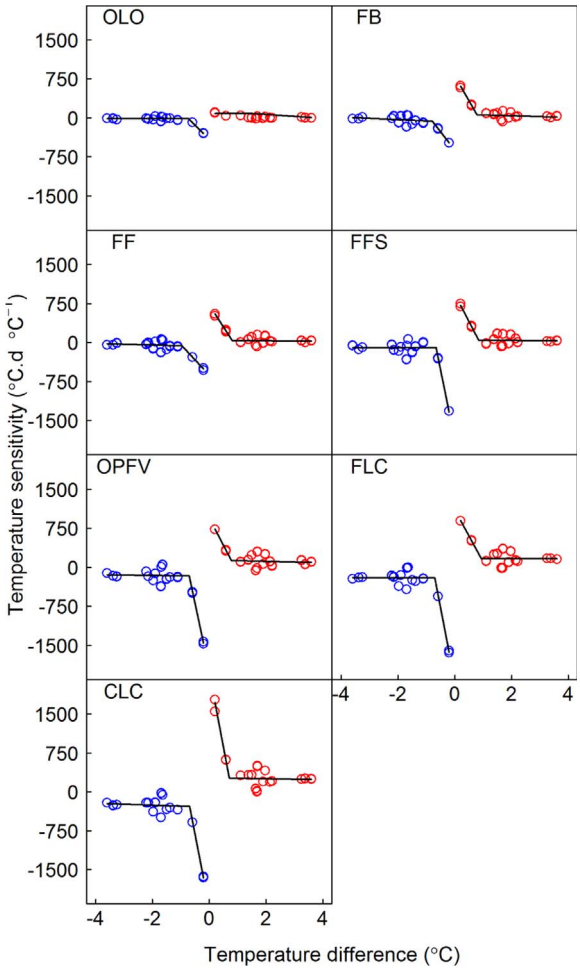

Fig. 4. Nonlinear regressions between temperature sensitivities of accumulated soil temperature (AST) and soil temperature differences. Each point represents temperature sensitivities of AST from one plot at specific year (6 and 33 for warming or 30 for cooling on two sides). Blue and red lines represent cooling and warming, respectively. The temperature change is difference between original site and transferred site for transplanted plants. OLO, onset of leaf-out; FB, first flower bud; FF, first flowering; FFS, first fruit-set for forbs or seeding-set for graminoids; OPFV, onset of post-fruiting vegetation; FLC, first leaf coloring and CLC, the date of complete leaf-coloring. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

our results show that changes in the temperature responses of SDI for different flowering functional groups could mediate the responses of temperature sensitivities of community phenophases.

In particular, we found that the temperature sensitivity of SDIESF had stronger correlations with the temperature sensitivities of community phenophases compared with SDIMSF under warming and cooling (Table 3). Changes in SDIMSF were not significantly affected by warming. Therefore, the temperature sensitivities of community phenophases were mainly influenced by the temperature sensitivity of SDIESF. This is in accordance with previous studies (Xia and Wan, 2013). This may indicate that changes in SDIESF played a primary role in the temperature sensitivity of community phenophases.

4.2. Biotic and abiotic factors cause nonlinear responses of temperature sensitivities of community phenophases

Consistent with previous reports (Iler et al., 2013; Meng et al., 2016b), our results found that nonlinear regression models best predicted future changes in phenology. Meanwhile, most nonlinear responses of temperature sensitivities of community phenophases declined quickly only up to a breakpoint, beyond which the temperature sensitivities of community phenophases remained relatively stable (Fig. 3). First, numerous studies have considered that the best explanation for nonlinear responses was plants adaptation to warming (Iler et al., 2013; Meng et al., 2016b; Piao et al., 2011), while few studies have focused on the effects of community composition and structure. We found that temperature responses of SDI for different flowering functional groups could modify temperature sensitivities of community phenophases, because there were significant positive or negative correlations between them (Table 3), and the values of their breakpoints were very close (Fig. 2 and 3). As a result, a rapid decline in the temperature responses of SDIESF and SDIMSF before breakpoints caused a rapid decline of the temperature sensitivities of nearly all community phenophases (Fig. 3). Similarly, the temperature sensitivities of nearly all community phenophases remained relatively stable after these breakpoints (Fig. 3). These results suggest that plant diversity had significant effects on the response pattern of community phenophases. Therefore, studies on community phenophases based on remote sensing and models should consider the effects of plant diversity.

In particular, we found that temperature sensitivities of community phenophases had relatively stable breakpoints (average breakpoint was ± 0.65 °C, Table S1 and Fig. 3) compared with species-level breakpoints (most breakpoints were more than | ± 1|°C) (Meng et al., 2016b). The stable breakpoint of community phenophases may be caused by mutual offset among all species, because different species had

Table 3
Partial correlations between temperature responses of SDI for three flowering functional groups and temperature sensitivities of the onsets of phenophases (n = 39 for warming, n = 36 for cooling), setting temperature changes as the controlling variable.

Phenophases	SDIESF		SDIMSF		SDILAF	
	Warming	Cooling	Warming	Cooling	Warming	Cooling
OLO	0.644**	0.658**	0.577**	0.228	−0.011	−0.162
FB	0.606**	0.744**	0.628**	0.340*	0.016	−0.21
FF	0.679**	0.732**	0.573**	0.264	0.02	−0.154
FFS	0.631**	−0.317	0.431**	−0.479**	0.045	0.425**
OPFV	0.647**	−0.524**	0.468**	−0.466**	0.024	0.410*
FLC	0.616**	−0.712**	0.530**	−0.493**	0.04	0.288
CLC	−0.533**	−0.667**	−0.537**	−0.317	0.043	0.193

Note: OLO, onset of leaf-out; FB, first flower bud; FF, first flowering; FFS, first fruit-set for forbs or seeding-set for graminoids; OPFV, onset of post-fruiting vegetation; FLC, first leaf coloring and CLC, the date of complete leaf-coloring. SDIESF, temperature sensitivity of Simpson's Diversity Index for early-spring flowering functional group; SDIMSF, temperature sensitivity of Simpson's Diversity Index for middle-summer flowering functional group and SDILAF, temperature sensitivity of Simpson's Diversity Index for late-autumn flowering functional group between receptor and donor sites, respectively.

* $P < 0.05$.

** $P < 0.01$.

divergent temporal niches and divergent response rates in the community (Godoy and Levine, 2014; Steltzer and Post, 2009; Wolkovich and Cleland, 2014). Our findings suggest that changes in SDIESF and SDIMSF could explain the nonlinear responses of temperature sensitivities of community phenophases. The nonlinear responses of temperature sensitivities of community phenophases may contribute to maintenance of long-term ecological fitness (Bennie et al., 2010).

Second, alpine plants are very sensitive to climate change (Arft et al., 1999; Jiang et al., 2016; Li et al., 2016; Wolkovich et al., 2012). Therefore, small temperature changes could significantly affect plant growth (Pieper et al., 2011). However, plants may acclimatize to climate change (Piao et al., 2011; Wang et al., 2014a). For example, similar to previous studies (Fu et al., 2014; Piao et al., 2011; Wang et al., 2014a), we found that the accumulated soil temperature requirements for community phenophases did not remain constant, which were significantly increased and decreased along with increased warming and cooling compared with control sites, respectively (Fig. 4). Thus, changes in community phenophases will depend on the difference between the rate of changes in temperature and the rate of change in accumulated soil temperature. For example, community phenophases were significantly advanced or delayed before breakpoints (Fig. 3), probably because rates of change in accumulated soil temperature were smaller than rates of change in temperature. However, the temperature sensitivities declined because of continued increase or decrease of accumulated temperature (Fig. 4). When passed breakpoints, the accumulated temperature kept constant (temperature sensitivity is nearly 0 °C.d °C^{-1}) along with continued warming or cooling (Fig. 4), the temperature sensitivities of community phenophases therefore remained stable (Fig. 3). These changes may be caused by a trade-off between temperature and accumulated soil temperature (Meng et al., 2016b). Therefore, plant adaptation to climate change by changing required accumulated soil temperatures could also affect nonlinear responses of temperature sensitivities of community phenophases.

There may also be other factors explaining declined temperature sensitivities before breakpoints, for which we propose two explanations. Firstly, we found temperature sensitivities of community phenophases declined under continued warming before breakpoints. It may be affected by chilling requirements, especially for early phenophases. Because increased temperature and accumulated temperature could cause a decrease in chilling requirement (Fu et al., 2015; Hart et al., 2014; Jochner et al., 2016), due to negatively correlations between chilling requirements and accumulated temperature (Cong et al., 2017; Fu et al., 2014). Chilling requirements is a long-term evolutionary adaptation of phenology to climate change (Fig S3), same as accumulated temperature (Wang et al., 2014a). But as we know there are no evidences that chilling requirements would change with climate change. Therefore, we assumed chilling requirements of plant phenology would not be changed after short-term warming compared with control sites. So warming (transferred downward) significantly decreased chilling days (Fig S3), which could then reduce the temperature sensitivities of early community phenophases under warming (Fu et al., 2015). Secondly, we found temperature sensitivities of community phenophases declined under continued cooling before breakpoints, especially for early and late phenophases. It may be affected by the photoperiod. Although they have approximately photoperiod due to short distance, interactions between photoperiod and temperature changes are divergent for plants from different elevations. Because they had different responses due to long-term adaptation of local elevation. For example, the same species had divergent GDD requirements at different elevations (Wang et al., 2014b), and community had divergent timings of phenophases between transferred and original sites at the same elevation (Fig S4). Therefore, even continued cooling significantly delayed phenophases in short-term, evolutionary experience (i.e., photoperiod) would still trigger phenophase (Körner, 2003) when a minimum photoperiod has been met in alpine plants (Hulber et al., 2010; Iler et al., 2013; Keller and Körner, 2003). This may be contributed to complete their life history because their phenophases were significantly later than original sites at the same elevation (Fig S4). Therefore, declined temperature sensitivities were the trade-off between cooling and photoperiod. However, there is no such problem under warming, because warming may significantly weaken the influence of the photoperiod (Heide, 1989), leaving plants with sufficient time to accomplish their life history. However, as for middle or late phenophases, their changes may be caused by early phenophases, because early phenophases had significantly positive influence on subsequent phenophases (Wang et al., 2014b).

5. Conclusion

In general, our results showed that nonlinear regression models were the best fitting models for the temperature sensitivities of Simpson's Diversity Index of early-spring (SDIESF) and mid-summer flowering species (SDIMSF) and of most community phenophases. In addition, there were significant correlations between them. Hence, our results indicate that SDIESF and SDIMSF combined with accumulated soil temperatures determine the response patterns of temperature sensitivities of community phenophases.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.01.034.

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